

ENTOMOLOGICA AMERICANA

VOL. XV

APRIL, 1935

No. 2

A STUDY OF MEDETERA ALDRICHII WH. (DIPTERA- DOLICHOPODIDAE), A PREDATOR OF THE MOUN- TAIN PINE BEETLE (DENDROCTONUS MONTI- COLAE HOPK., COLEO.-SCOLYTIDAE)

BY DONALD DE LEON, BERKELEY, CALIFORNIA

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INTRODUCTION

The larva of this fly is the most common and valuable predator on the brood of the mountain pine beetle in lodgepole pine, western white pine, and probably ponderosa pine in Montana, Idaho, and eastern Washington. A great deal more study is required on the biology and habits of the enemies of barkbeetles, as there is serious danger of abetting the barkbeetle outbreaks in the long run, when control work is carried out and no attempt is made to protect the beneficial insects.

No previous studies have been recorded concerning this species, nor has the morphology or biology of any species of this genus been fully worked out in Europe or America.

The morphological portion of this paper was worked out in the laboratory of Cornell University. Grateful acknowledgment is made to Professor O. A. Johannsen for his constant aid and advice. Acknowledgment is also made to Mr. W. D. Bedard for sending me living material from northeastern Washington; his cooperation was a great aid in the satisfactory outcome of the problem. The biological notes were secured during the summers of 1929 and 1930 in the lodgepole pine regions around Sula, Montana, and the western white pine regions in northeastern Washington near Metaline Falls.

SYSTEMATIC POSITION AND SYNONYMY

Keen (1928). *Medeterus aldrichii* Wh.

Medetera aldrichii Wh. belongs to the family Dolichopodidae, one of the higher families of the Diptera-Brachycera. The genus *Medetera* was described by Fischer von Waldheim (1819). It is placed by Aldrich (1905) in the subfamily Medeterinae. Wheeler (1899) described this species from material collected at Moscow, Idaho.

PREVIOUS STUDIES ON THE MORPHOLOGY AND BIOLOGY
OF THE GENUS

There are many miscellaneous records that mention the finding of larvae or pupae of *Medetera* under the bark of trees, and the observing of the adult feeding on some smaller insect.

Damianitsch (1865) was apparently the first to figure an immature stage. He figures and describes the cocoon of *M. tristis* Zett. and states it was found in a tree containing barkbeetles. Perris (1870) describes and figures the larva, the pupa, and the cocoon formation of *M. ambiguus* Meig. His description of the former

stage is rather complete but he states that the rows of spicules on the pseudopodia are at the posterior margin of the segments and not at the anterior margin where actually they are. He believed it to be predacious on *Ips*. Kowarz (1877) in a systematic paper mentions that several species have been reared from trees infested with barkbeetles. Mention is made of the cocoon. Brauer (1883) describes the larvae of the Dolichopodidae in general, and speaks of the cocoon of *Medetera*. Hopkins (1899) believed *M. nigripes* Lw. to prey on *Polygraphus rufipennis* (Kby.) in spruce. Kleine (1907) gives a brief account of the larva, pupal case, and pupa of *M. obscurus* Egger but states that the adult enters beetle exit holes to oviposit. He thought that the larva might be predacious, and states that the adults are predacious. The larva, he adds, forms its cocoon near a beetle exit hole through which the adult emerges after transformation. A larva of *Medetera* is recorded by Felt (1911 and 1913) preying on *Miastor* larvae. Lundbeck (1912) briefly reviewed what was known on the biology of the group as a whole. He states that all the Dolichopodidae are predacious in the adult stage. Trägårdh (1914) speaks of the predacious habit of the larvae of *M. signaticornis* Lw. and gives a figure of the larva and its head structures. DeMeijere (1916) goes into considerable detail in figuring and describing an unspecified larva and pupa of *Medetera*. It is the best work that has appeared on the structures of the mouth parts. Malloch (1917 and 1917a) observed a *Medetera* feeding on a male *Forcipomyia*. The same author (1919) collected larvae of an undescribed species of *Medetera* under the bark of cottonwood. He mentions the formation of a cocoon. Blackman and Stage (1918) record an undetermined species of *Medetera* having been reared from beetle-killed larch trees. Mokrzecki (1924) mentions *M. signatoricornis* as preying on the larvae and pupae of *Ips typographus* (L.). Hubault (1923) believes that *M. signaticornis* feeds on the larvae of *Ips curvidens* (Germ.). Seitner (1924) figures several stages of *M. signaticornis* and gives some brief notes on the biology and habits. The first fairly detailed discussion of *Medetera* is that given by Hubault (1925). He comes to the conclusion that *Medetera pallipes* is both xylophagous and predacious, claiming that he has found particles of wood in the digestive tract of the larva. He also observed larvae of the same species feeding on the brood of barkbeetles. *M. signaticornis*, he says, oviposits in the frass in beetle exit holes, and *M. pallipes* enters the beetle gallery so far as to pass out of sight. He describes

briefly the egg, the larva, and its mouth parts. Curran (1928) in descriptions of several new species of *Medetera* records them as having been reared from decaying oak and chestnut bark. Keen (1928) mentions that the larval stage of *M. aldrichii* is predacious on the brood of *D. monticolae*, and probably other barkbeetles in western yellow pine and lodgepole pine. Taylor (1928) records an undetermined *Medetera* having been reared from leaders of white pine infested with the white pine weevil (*Pissodes strobi* (Peck)). Schimitschek (1931) says that *M. excellans* Frey, in the larval state, is predacious on *Ips cembrae*. He describes the pupa, gives the pupal stage (10–14 days), and adds that the larvae overwinter in a J-shaped position. He believes that at times there may be two broods a season.

DESCRIPTION OF STAGES

EGG

The eggs are oval in shape, slightly convex above, concave below; brownish orange in color, smooth, and shining. Those taken from lodgepole pine in Montana averaged 0.86 mm. in length and 0.18 mm. in width; those secured from white pine in Washington were slightly larger. The average size of the sixteen eggs from this region is as follows: length, 0.91 mm.; width, 0.21 mm.; maximum length, 0.99 mm.; maximum width, 0.25 mm.; minimum length, 0.81 mm.; minimum width, 0.18 mm.

LARVA

First Stage

The first instar larvae are slender, creamy white in color, and average about 0.7 mm. in length. They are metapneustic. The number of body segments was not determined. There are no sclerotized areas on the head or first thoracic segment.

Second Stage

The second instar was not observed for this species. The larvae of *M. signaticornis* Loew, which were studied by the writer with greater care, went through three instars, and it is probable that there is the same number for *M. aldrichii*. The second instar of the former species resembles the first instar in lacking the sclerotized areas of the head and first thoracic segment.

Last Stage

General Structure

The full-grown larvae (Pl. 4, A) are amphipneustic and average 8.5 mm. in length. They are roughly cylindrical in shape, and are composed of an apparently subdivided head, three thoracic and eight abdominal segments. Body segments five to ten are subdivided at the anterior margin, forming a narrow ring on all sides except the ventral. Segment 10 is about 1.4 times as long as segment nine, and about 2.5 times as long as segment 11. Each of the abdominal segments, except the last, bears a ventral pseudopodium (Pl. 4, A, ps) provided on each side with an anterior transverse row of 9 to 11 bidentate rugosities (Pl. 5, B, ce), which range in length from 0.045 to 0.066 mm., and with 7 to 9 semi-concentric rows of smaller spicules (Pl. 5, B, ei). The inner end of each row composed of rugosities of type ce is terminated by a spicule of type eg. Between the two spicules of type eg there is a small scabrous area, cf. In the middle of each pseudopodium caudad to area cf and between the rows of spicules of type ei, one finds a rugosity of a fifth type, ch. This rugosity is 2 to 4 lobed. The rugosity of type ch is often absent from the pseudopodium of segment 4 and the other spicules of this pseudopodium are frequently less strongly developed than those on the other pseudopodia.

The caudal region of the dorsum of the head bears a brownish sclerotized area roughly oval in shape. The cephalic position of the dorsum of the first thoracic segment bears a similarly situated but a much narrower sclerotized area. The cephalic pair of spiracles are small. They are situated below the median lateral, longitudinal line and behind the median transverse line of the prothorax.

The anus opens as a longitudinal slit on the ventral surface of, and slightly anterior to, the middle of segment 11, in a more or less circular pad-like swelling of the cuticula (Pl. 4, A, ap). A series of sclerotized cuticular processes border the margin of the pad and extend laterad as shown in Pl. 4, B, cp. The arrangement and position of these processes varies considerably in different larvae and often in the same larva the spines of the left side are not arranged the same as on the right. The end of this segment is cut dorso-ventrally by a median groove and laterally, slightly above the middle by a transverse groove, thus forming four protuberances. The two ventral protuberances project beyond the dorsal ones so that the former can be seen when viewed from above. They are likewise closer together and more sharply tapered than

the dorsal pair of protuberances. The spiracles (Pl. 4, F, sp) of this segment are much larger than the anterior pair, more strongly pigmented with brown, roughly oval in shape, and have two large oval openings into the stigmatic chamber. The length of the long axes of the caudal spiracles is about 0.04 mm.; that of the short axes about 0.03 mm. The dorsal and lateral areas around the spiracles are slightly sclerotized and four branched spines are located in this region close to the margin of the spiracles as shown in Pl. 5, D. Spines of similar form and position have been mentioned by numerous authors for various families of the Cyclorrhapha. Snodgrass (1924) shows that their form varies in each of the three larval instars of *Rhagoletis pomonella* Walsh.

Description of the Head and Its Appendages

Since the homologies of the mouth parts can only be worked out by a histological study of the early stages of several groups of larvae, the terminology used in describing these parts is that employed, for the most part, by DeMeijere (l.c.). The development of the mouth part and head of a cyclorrhaphous larva and a review of the literature pertaining to the subject in general have been made by Snodgrass (l.c.). In the higher diptera of the Brachycera the tentorial and metacephalic rods may be the forerunners of the posterior lateral plate and the dorsal wing, respectively, of the pharyngeal skeleton of the cyclorrhaphids as described by Snodgrass. The median piece may be the so-called median hook greatly modified that is present in only the first stage larvae of many cyclorrhaphids. The oral hooks of this latter group may be the mandibles of the higher Brachycera.

The head of *M. aldrichi* (Pl. 5, I) is about 0.3 mm. in length. It is completely and permanently exerted and divided dorsad into an anterior and posterior region by a transverse suture that is absent on the ventral surface of the head. The posterior division is about one and one-half times as long as the anterior division and bears an oval pigmented area occupying nearly the whole of the dorsum. The anterior division of the head is produced forward in the form of two lateral lobes, which are separated from the rest of the head by a complete suture. These lobes bear the mandibles, palpi, and other sensillae. They can be deflexed independently to form almost right angles with the body. The antennae are borne on a pair of lateral lobes of the anterior head division. Each antenna is composed of three types of sensillae, as shown in Pl. 5, I, ana, in-

serted anterior to a brownish pigmented plate that is apparently set down into the cuticula.

The exact nature of the antennal sensillae could not be established. One is a transparent, globe-shaped papilla with a disk at its tip and a cylinder-like "channel" extending from the disk to the cuticula; one is a cylindrical, heavily pigmented papilla, with a hemispherical top, and the third is a narrow "papilla" with a bend near its base. The pigmented plate at the base of the antennal sensillae bears at the outer angle of its caudal prolongation three more sensillae. On the ventral surface of the anterior division in the region of the antennae six pairs of sensillae are located. Two pairs form surface papillae, three pairs appear only as sclerotized rings, and one pair only as a sensilla without any external markings, but showing through the cuticula as a bottle-shaped organ. The sensillary organ near the inner caudal margin of the antennal plate is about 0.0058 mm. in diameter.

The maxillary palpi (Pl. 5, I, r, and p) are located at the outer tip of the maxillary lobes. The palpi are composed of two pigmented, roughly cylindrical bodies, one dorsal to the other. The upper one is distinctly larger than the lower and each one bears a pair of sensillae. At the outer margin of the palpi on the ventral side, another sensilla is located. Dorsad on the inner margin somewhat in front of the end of the mandibular hook a second sensilla is present, and on the outer margin slightly behind the middle of the maxillary lobe another sensilla can be found. A fourth sensilla is present on the ventral surface of the posterior division of the head located as shown in the figure (Pl. 5, I, s_3). The pigmented areas lettered x and y in the aforementioned plate are apparently of cuticular origin and cannot be dissected out with the mouth parts.

The sclerites that go to make up the internal mouth parts consist of two groups: (1) the median piece (Pl. 5, C) and its parts, *i.e.*, the tentorial and metacephalic rods (Pl. 4, A, t & m), and (2) the mandible and its parts (Pl. 5, E). The median piece is about 0.166 mm. in length, 0.15 mm. in width, and 0.089 mm. in height. When viewed laterally it is roughly triangular in shape. The size of the mandible and its parts are as follows: mandible, length, 0.08 mm., width, 0.027 mm.; vertical sclerite, length, 0.066 mm., width, 0.03 mm.; dorsal sclerite, length, 0.077 mm. In Plate 5, the figures C, F, and I have the corresponding parts lettered the same. The blunt teeth (e) of the median piece vary in number. In some specimens two pronounced teeth were present; in others only a slight elevation indicated the presence of the second tooth.

The larvae have been observed in the act of attacking their prey many times; the action of the mouthparts seemed to be as follows: at the time of attack the anterior tip of the median piece is pushed forward and upward by the pressure from the tentorial rods. The rods are forced forward by the powerful longitudinal pharyngeal muscles attached to them. At the same time the mandibular hooks work down and out, catching into the cuticula of the prey. The pressure exerted by the forward and upward movement of the end of the median piece and the downward movement of the mandibles is sufficient to rupture the cuticula. The fluids of the prey are then sucked up by means of the strong vertical pharyngeal muscles pulling on the dorsal wall of the pharynx, which is distinctly sclerotized and bears many small oval rugosities for the attachment of the muscles (Pl. 5, F & G, ph). In Plate 5, F, these rugosities are shown diagrammatically through the ventral wall and the number is actually about twice as many as is shown per unit area. The inner ventral surface of the tentorial rods is grooved, permitting the insertion of the sides of the lower floor of the pharynx (Pl. 5, G, t).

Sensillae of the Body

A very definite arrangement of sensillae has been found on the body segments. Pantel (1898) is apparently the first to mention these organs for dipterous larvae. The presence of sensillae on the cuticle of dipterous larvae of the Nemocera, Brachycera, and Cyclorrhapha has been discussed by Keilin (1911). He discusses especially what he calls the "formation d" and to which Thompson (1920) has given the name Keilin's organ. A pair of these organs is situated on the ventral surface of the three thoracic segments, each organ consisting of 4 spines surrounded by a cuticular ring. According to Keilin they represent the portion of the legs in the ancestors of the present-day larvae. In the work quoted, Keilin shows that although the length of these spines varies with the family or genus the number is constant. In fact, from his list, though he does not state this himself, one notices that all the Cyclorrhapha except the phorids have three spines, all the Orthorrhapha four spines. The Phoridae, in a special study of Keilin (1911a) are placed with the Cyclorrhapha, although there are four spines in "organ d." The position of the phorids, however, is an uncertain one; various authors place them in the Orthorrhapha, others in the Cyclorrhapha, and still others in with the Pupipara.

The position of the body sensillae of *M. aldrichii* may be observed by a study of Pl. 4, B. The sensillae are composed of three

types; organ a_1 , *organ en cercle* of Keilin; organ c_1 , which has the shape of a depressed papilla rather than the rod-like type described by Keilin for the phorids, and organ d_1 , which is composed of four spines located on the ventral surface of the thoracic segments. Organ a_1 appears as a thickened oval-shaped ring of cuticula with a circular center. On the first thoracic segment these rings are somewhat wider, more heavily pigmented, and slightly larger than on the succeeding segments. Organ a_1 of segment 1 is about 0.0088 mm. in length; on segment 2 it is about 0.0055 mm. in length. Organ c_1 appears to have no cuticular thickening surrounding it at the surface, but its channel through the cuticula is more heavily pigmented and in either the primary or secondary cuticula it enlarges, forming a somewhat circular base. This organ, when viewed vertically or at a slight angle, appears at first sight to be like Keilin's organ c , or "*organ en batonnet*" but when viewed from the side, in profile, it appears as a flattened papilla. The diameter of this organ on segment 1 is 0.0055 mm. It is present on segment 2 but could not be found on segment 3 or on the abdominal segments save the last. Here two pairs of organs occur dorsad and one pair ventrad that are the same as, or closely resemble, organ c_1 . The dorsal surface of the lower pair of terminal lobes of this segment bears a branched spine and two sensillae that lack the cuticular rings.

Internal Anatomy

Tegumentary Muscles

The integumentary muscle system was studied in detail only for segments 6 and 7. Plate 6, B and C, show the muscles of these segments viewed laterad towards the outside. Figure B shows the outermost sets of muscles, figure C the innermost sets, except the vertical muscles (v), which are the same in both figures. The broadest muscles of the innermost set measured about 0.071 mm. in width in the specimens examined. It seems well to call attention to the branched muscles found in the abdomen. The uppermost muscle (dvdo, Pl. 6, C) has one strand that originates at the posterior margin of the secondary segmentation of the segment, and one strand that originates at the anterior margin of the same secondary division. An idea of the complicated muscle system of the thorax in the region of the pharynx can be obtained by a study of Plate 5, G, which is a cross section slightly anterior to the prothoracic spiracles. The arrangement of the muscles in segment 13

is quite complicated. The most interesting point, however, is the large transverse muscle (Pl. 4, C, tr) extending across the body from one side to the other, slightly anterior to the rectum and over which it bends at nearly a right angle to reach the anus.

Digestive System

(Plate 4, C)

The fore-gut consists of the mouth, the pharynx that extends to near the middle of segment 2, and the oesophagus that begins at this point and narrows to about 0.03 mm. in diameter at its narrowest. At the brain it makes a sharp turn dorsad, passing between the two lobes of the brain that are united dorsad. The oesophageal valve is in the extreme anterior portion of segment 4. It is about 0.1 mm. in diameter. The mid-gut extends from the valve into segment 8, where it turns ventrad and then forward, enlarging until it reaches the hind-gut in the posterior part of segment 6. At its narrowest part the mid-gut is about 0.04 mm. in diameter, at its widest part it ranges from 0.06 mm. to 0.25 mm. in diameter. The hind-gut turns dorsad, as a narrow tube which enlarges into the colon in segment 9. At the posterior margin of segment 10 it narrows into the rectum and turns vertically downwards over the transverse muscle and ends at the anus. At its greatest diameter the rectum is about 0.1 mm. in diameter.

Four Malpighian tubes are present at the union of the mid- and hind-guts. One pair runs cephalad into segment 5 and then turns back, ending, as far as could be determined, in segment 6. They are considerably convoluted and border for the most part the sheets of the fat-body. The remaining pair extends caudad along the edges of the fat-bodies. This pair is much more convoluted than shown in Pl. 4, C. In sections, traces of them can be found in segment 11.

The salivary duct unites with the fore-intestine at the anterior part of the pharynx. It extends as a common duct into segment 2, where it branches, a branch passing on either side of the brain. In segment 3 it unites with the salivary glands which extend back into segment 9. They are much enlarged in segments 4 and 8 and considerably constricted between these segments. They are about 0.1 mm. in diameter at their narrowest part and 0.4 mm. at their greatest diameter. In sections of specimens stained with eosin and Delafield's hematoxylin the contents of the anterior enlargement stain blue, and appear to have a fibrous texture. The contents of

the posterior enlargement stain a uniform red and show no indication of a fibrous matrix. The epithelial cells of the wall are large, hexagonal, and contain large nuclei.

Respiratory System

The network of tracheae of *M. aldrichii* has an interesting arrangement. It resembles that of the average cyclorrhaphid larva (Hewitt, 1908), (Keilin, 1915), (Gaebler, 1930), (Ruehle, 1932), more than the lower groups of diptera as the Tipulidae (Hinkley, 1930), for example. However, the tracheal system of the orthorrhaphid, *Cecidomyia resinicoloides* Williams (Williams, 1910) is also of the cyclorrhaphid type, so that it is difficult to generalize. These similarities and differences between the two types can be attributed chiefly to the cephalization of the nervous system, as pointed out by Ruehle (l.c.). In the larvae with a cephalized ventral nervous system the tracheae that aerate the ganglion for each body segment are pulled forward or backward to the centralized ganglia, while in larvae provided with a ganglion in each segment, there is no need for these modifications.

The arrangement of the respiratory system of *M. aldrichii* can best be understood by a study of Plate 4, D, E, and F. The tracheae discussed below are of particular interest.

In segment 11 a pair of tracheae (vt) branch from the lateral posterior branches and extend forward and somewhat ventrad, crossing each other in segment 10, and then run alongside of each other, so that it is difficult to keep track of which one arose from the left side and which one from the right side. Both tracheae, however, extend cephalad into segment 8. Here trachea vt of the left side ends by branching in the caudal half of this segment, the branches ending in the tissues of the digestive tract. Trachea vt of the right side branches in the same manner in the extreme caudal region of segment 7 but one of these branches continues cephalad along the digestive tract for about another segment. In making dissections of fresh material to study the digestive tract, a large trachea coming somewhere from the posterior part of the insect was always found to lose itself by branching at the union of the mid- and hind-guts, and it is probable that this trachea is trachea vt of the right side. Hewitt (l.c.) and Williams (l.c.) show what are apparently homologous tracheae in the larva of the housefly and pitch gnat, respectively.

The ventral tracheal system of the thorax is shown in Plate 4, D. Each of the ventral thoracic commissures (vtc 1-3) give off

a pair of caudad extending tracheae, the thoracic ganglionic tracheae (tgt 1-3), that run back to, and lose themselves by branching in the cephalized part of the nervous system. The abdominal ganglionic tracheae (au 1-4) are likewise shown in the figure, which is semi-diagrammatic, for it could not be determined exactly what parts of the nervous system were supplied by each trachea. Altogether, the cephalized nervous system is supplied with air by 8 pairs of tracheae. Seven pairs extend ventrad to it and one pair extends down between the brain lobes (brain tracheae bc, Pl. 4, E). This pair arises from a pair of tracheae originating slightly anterior to the anterior dorsal commissure (ac) and extending ventrad and caudad a slight distance. Here it branches into three tracheae. One of these extends backward as the brain trachea and is connected by a commissure with the corresponding trachea on the other side. The other two tracheae run caudad a short distance, then turn sharply down and forward. One of these remains unbranched, the other branches once and one of these branches divides into two and then all four tracheae lose themselves in the muscles of the pharynx, consequently in Plate 4, E, these tracheae (ph 1-4) are shown incomplete.

The diameters of a few of the tracheae are summarized below:

Longitudinal trunk (lt) behind posterior commissure = 0.0288-0.0399 mm.

Longitudinal trunk (lt) behind anterior commissure = 0.023 mm.

Ventral thoracic commissure 1 (vtc 1) = 0.0058 mm.

Ventral thoracic commissure 2 (vtc 2) = 0.0088 mm.

Anterior commissure (ac) = 0.0136 mm.

Lateral branch near base = 0.01 mm.

Circulatory System

The heart extends dorsad as the aorta and then caudad from the brain in segment 3 to the anterior part of segment 11. In sections it appears somewhat larger posteriorly. The diameters ranged from about 0.033 mm. to 0.05 mm. The number of valves of the heart was not determined.

Adipose Tissue and Urate Cells

The adipose tissue lies in long layers, one cell thick, on either side of the abdomen. When fresh material is dissected the Malpighian tubes are always found to be bordering one of these layers. The urate cells are not distinctly visible through the cuticle of the larvae so that their abundance and position were not determined.

Nervous System

The nervous system (Pl. 9, C) consists of a group of ganglia centralized in segments 3 and 4. At least four pairs of nerves run cephalad from the region below the brain and from the extreme caudal end of the cephalized area a "strand" of nerves can be traced caudad, to the posterior region of segment 10. In a few of the segments a pair of nerves could be found apparently turning off from the main "strand" at about a 60° angle. It was not established whether a pair provides for each abdominal segment but this is probably the case. No fan of nerves was observed extending from the mass of consolidated ganglia as is present in the house-fly (Hewitt, l.c.) and other cyclorrhaphids.

COCOON

The cocoon of *Medetera* is dirty whitish in color, and at times resembles a small cocoon of *Coeloides* so closely that at a glance it is difficult to be certain which species one is observing. The cocoons are about 5 mm. in length and oval in shape.

PUPA

The pupa (Pl. 6, A) is creamy white in color except for the brownish sclerotized areas. The average length is about 4.5 mm., the average width about 2 mm. A pair of sclerotized respiratory spines originate directly behind the eyes, and their bases extend parallel to the posterior margin of the eyes beneath the cuticula. A single transverse row of spines is found dorsally on all but the terminal of the last eight body segments. A pair of spiracles or spiracular scars are found on each, except the last two of the segments bearing the row of spines. The terminal segment bears a series of 5 to 7 pairs of elongated spines; and an inner and much shorter pair; all but the inner and shortest pair are hooked at the end. In front of each row of dorsal abdominal spines is an area of innumerable, minute, sharply pointed spines that diminish in number towards the anterior margin of each segment. Laterad, the spines become slighter but on the lateral swellings they are larger, forming distinct scabrous areas. No scabrous areas are found on the thorax but 3 pairs of small spines are present, located as shown in Pl. 6, A. The anterior spine may in some instances be doubled, so that on one side of the pupa two spines may be present where there is normally one.

The drawing of the pupa shows the extremities of the metathoracic legs extending to the middle of the antepenultimate seg-

ment. Actually, the legs reach the middle of the penultimate segment but the pupa, when drawn, was somewhat extended, owing to the pressure of the coverslip.

ADULT

The adult (Pl. 7) is a somber grey fly averaging about 4 mm. in length. There is, however, a slight bluish-green sheen to the body when the light strikes it at certain angles, and the front below the antennae is distinctly blue-green. The basal joint of the antenna is orange; the second and third segments are black. The thorax is marked dorsally by four greyish-white vittae, and the scutellum bears two pairs of bristles. The cubital cell of the wing is short and not pointed. The second segment of the tarsus of the metathoracic leg is not more than twice the length of the first; while in the first two pairs of legs the first joint of each tarsus is longer than the second.

SEASONAL HISTORY, BIOLOGY, AND HABITS

Acknowledgment is made to Dr. F. C. Craighead of the Bureau of Entomology for permission to publish these notes and to Mr. J. C. Evenden of the same Bureau, under whom the writer worked, for his constant aid and advice during these investigations.

INCUBATION PERIOD

The eggs hatch after an incubation period of ten to fourteen days. Just before the eggs hatch the larva can be seen through the chorion in a J-shaped position, with the head at the longer end of the "J."

LARVAL DEVELOPMENT

After hatching, the larvae work their way into the inner bark in search of nourishment. They feed chiefly on the eggs, larvae, and pupae of the mountain pine beetle, but they will also feed on dead ones, on small cerambycid larvae, and on each other. They cannot be reared together, for within a few days only one will be left.

An attempt was made to rear the larvae in decaying cambium, and while some lived for nearly a month, all died without appreciable growth. It shows, however, that although they are capable of living for a considerable period without animal food, they probably require this for development. The writer from the study of the mouth parts of both European and American species does not be-

lieve that *Medetera* can feed on wood as suggested by Hubault (1925). It may be possible to find traces of wood fiber in the digestive tract of these larvae, but in this case it seems more reasonable to assume that the fibers were sucked up by the larva during feeding on scolytid larvae.

The larvae of *Medetera aldrichii*, it seems, find their prey fortuitously. In the laboratory they have been observed to pass by, almost touching the larvae of *Dendroctonus monticolae* or the larvae of their own species, without apparently sensing the others' presence.

Under laboratory conditions the predators were never observed to feed continuously on the larva on which they started to feed. Whether it is due, perhaps to a passing whim, or to having had enough nourishment for the time being, they seldom fed long. In the vial, of course, the partially-consumed larvae could be chanced upon again, fed upon for a while longer until in the end they would be reduced to nothing but their integument.

The larvae were found at all times of the year in trees ranging from those newly attacked, to trees recently abandoned by the mountain pine beetle, but they were most numerous in recently infested trees. As they prefer moist conditions under the bark, they were seldom found in any numbers in trees abandoned by the beetles. The soft inner bark of infested trees usually begins to dry out when the brood is still in the callow adult stage, and by the time the beetles have emerged it is generally extremely dry. Though the small larvae work chiefly between the wood and the bark, the larger larvae are often equally numerous in the soft inner bark, where they are entirely concealed.

The larval period is not definitely known; while at times it is as short as about a month, it often occupies ten to eleven months. In any case, it certainly appears to be less than a year.

FORMATION OF COCOON

Before pupation the larvae usually construct small cells composed of frass and shreds of cambium, and line the inside with a silk-like substance. A small opening in the cocoon is generally present at the anterior end. The cocoons are always in the soft inner bark, but may be either visible or concealed when the bark is removed. Though the cells are not always formed, the larvae always enclose themselves within the silk-like cocoons. Within the cocoons the larvae assume a J-shaped position and remain thus until pupation.

If the larvae were removed from the cocoon they did not spin a new one but died after a few weeks. In working with an undetermined species of *Medetera* from Ithaca, it was found that if the cocoon was broken open the larva would usually repair the break, even though the cocoon was ruptured after each repair.

PUPAL PERIOD

Pupae were found from May 7 to September 12 in the lodgepole pine type; in the white pine type they were found between April 25 and July 19, and probably could have been secured during August and September if a more extensive search had been made. Though the main period of pupation in lodgepole pine was between June 21 and July 19, no definite period of pupation was noted in western white pine.

The stadia of pupae for which the period was definitely known occupied 14 to 17 days. As none of the pupae collected in the field and reared even approached this period, it indicates that seventeen days is probably the maximum period required for development by this stage.

The terminal spines mentioned in the description of the pupa probably serve to anchor the pupal skin to the cocoon, thus enabling the adult to emerge from the pupal exuviae with less difficulty.

EMERGENCE OF ADULT

It has often been a wonder to the writer how these delicate flies can push their way through the cambium to the outside. Kleine (l.c.) says that *M. signaticornis* pupates near a beetle exit hole but the writer did not notice any such tendency with *M. aldrichii*.

FEEDING OF THE ADULT

Malloch (1917) and other authors report the adults feeding on smaller insects. The writer in one instance observed a female capture and feed on a small red-spider.

COPULATION

Though the courtship of some of the Dolichopodidae is very elaborate as described by Aldrich (1894) and Van Duzee and others (1921), the courtship, if any, and the mating of *Medetera aldrichii* were not observed. During observations on another species, *M. signaticornis* Lw., one fly was often observed to alight on the back of another without any preliminary maneuvers, but no copulation

was observed and the flies could not be caught to determine their sex.

OCCURRENCE AND OVIPOSITION

In the white pine stands the first adult was found on May 27, 1930; in the lodgepole pine stands the first adult was found on June 5, 1929. After these dates adults were present in the field the remainder of the season.

The imagines are rather ubiquitous, for they were observed on Douglas fir, cedar, western white pine, and lodgepole pine trees whether green or infested by barkbeetles. More extensive search would probably have disclosed their presence on other species of trees. Adults were found to be much more numerous, however, on infested trees, and especially so on trees that had been recently attacked by the mountain pine beetle. This was pronounced in one case of a white pine where, on a tree that had been attacked but two or three days previously, six or seven adults could be seen to a square foot of bark surface; whereas, on several trees near-by that had been attacked about eight days earlier, only two or three adults were observed over an equal area.

The female works over the bark in a rather interesting and amusing manner. She appears to glide in an effortless fashion forward, sideward, and backward with equal ease and frequency, and occasionally makes short hops from one place to another. Now and then she stops to feel under a bark scale or into a crevice with the tip of her ovipositor. Though she goes through the same actions on green as well as infested trees, no eggs have so far been found on green trees. On infested trees the eggs are laid singly or in clusters of two or three; no more than three in a group have been found in the field, but in the laboratory as many as nine eggs were laid in a scattered group. The eggs are placed under loose bark scales or in small crevices, never in ventilation or exit holes constructed by the parent mountain pine beetle. If a female *Medetera aldrichii* chances upon one of these holes she avoids it by moving to one side or flying off. There are, however, several smaller species of *Medetera*, as yet undetermined, which are occasionally found on trees infested both by the mountain pine beetle and other barkbeetles. These have only been observed to oviposit in ventilation or exit holes. Unfortunately, nothing is shown of the biology of these flies.

REPRODUCTIVE CAPACITY AND LENGTH OF LIFE

It is not known how many eggs a female lays during her existence. Dissection of a female collected in the field revealed four eggs practically mature and ready for laying; thirty partially formed in one ovary and thirty-one in the other, making a total of sixty-five eggs potentially for one female. This, of course, does not take into consideration the eggs laid before capture or the other eggs that may have developed if she had not been dissected. Females kept in the laboratory and fed on sugared water lived about three weeks; the males usually lived a shorter period.

OTHER HOSTS

Table 1 shows the record of collections of the larvae of *Medetera* from galleries of other barkbeetles or other host trees of the mountain pine beetle. As several other species of *Medetera* have been found on trees infested by various barkbeetles it is probable that the records in the following table include species other than *Medetera aldrichii*.

SECONDARY PARASITES OR OTHER ENEMIES

No enemies of the immature stages have been found. Lundbeck (l.c.) states that no hymenopterous enemies have been recorded for any of the Dolichopodidae. Under confinement the larvae are cannibalistic, but it is doubted if this normally occurs in the field.

Adults have been occasionally observed caught in spider webs and in one instance one of the non-web-spinning species of spiders was seen to capture a female *Medetera*.

ECONOMIC STATUS

To date the writer has been unable to determine the amount of brood of the mountain pine beetle destroyed by the larvae of *Medetera aldrichii*. As they move from host to host, it will take a considerable amount of controlled experimentation to determine how many individual eggs, larvae, and pupae each one destroys. The single controlled attempt made to determine the possible amount of brood destroyed by the larvae was unsuccessful. In addition, since they do not confine their attacks to the brood of the barkbeetle, each larva counted cannot be considered to have maintained itself entirely on the brood of the barkbeetle alone.

Bark from a western white pine tree that had been attacked by the mountain pine beetle about July 12, 1930, was examined for *Medetera* larvae July 26, 1930. In 39 cm. of gallery, 73 niches

TABLE 1. LIST OF HOST TREES AND INSECT GALLERIES FROM WHICH LARVAE OF THE GENUS *Medetera* HAVE BEEN SECURED*

Date of collection	Locality	Host tree	Insect gallery from which collected
May 4, 1929	Sula, Mont.	<i>Pinus contorta</i> Loud.	<i>Ips oregoni</i> (Eichh.)
June 23, 1929	" "	<i>P. albicaulis</i> Engel.	<i>Dendroctonus monticolae</i> Hopk.
June 30, 1929	" "	<i>P. ponderosa</i> Laws.	" "
Aug. 22, 1929	" "	<i>Abies lasiocarpa</i> (Hook.) Nutt.	<i>Dryocoetes confusus</i> Sw.
Sept. 19, 1929	Glacier N. P., Mont.	<i>Larix occidentalis</i> Nutt.	<i>Dendroctonus pseudotsugae</i> Hopk.
Sept. 30, 1929	Coeur d'Alene, Ida.	<i>Abies grandis</i> Lind.	<i>Hylurgops</i> sp.
Oct. 22, 1929	Lolo Hot Springs, Mont.	<i>Pinus contorta</i> Loud.	<i>Othotomicus caclatus</i> (Eichh.)
April 26, 1930	Metaine Falls, Wn.	<i>Abies grandis</i> Lind.	<i>Scolytus ventralis</i> Lec.
May 3, 1930	" "	<i>Pseudotsuga taxifolia</i> (Poir.)	<i>Dendroctonus pseudotsugae</i> Hopk.
May, 1930	Coeur d'Alene, Ida.	<i>Pinus ponderosa</i> Laws.	<i>Dendroctonus brevicornis</i> Lec.
June 19, 1930	Metaine Falls, Wn.	<i>Abies grandis</i> Lind.	<i>Dryocoetes confusus</i> Sw.
July 30, 1930	" "	<i>Pinus monticola</i> Dougl.	<i>D. affaber</i> (Manh.) and <i>Polygraphus rufipennis</i> (Ky.)

* Collections from the larval galleries of *Dendroctonus monticolae* Hopk. in lodgepole pine and western white pine are not included. After the above table was compiled, larvae of *Medetera* have been found in California in western white pine in the galleries of *Ips latidens* (Lec.), in sugar pine in the galleries of the mountain pine beetle, and in red fir and white fir in the galleries of several species of *Scolytus*.

were counted, of which 50, or 68 per cent, contained beetle eggs. Sixteen first instar larvae of *Medetera* were counted either feeding on the eggs or near the empty egg niches. It seems likely that these larvae destroyed all of the missing eggs and would probably have destroyed 40 to 50 per cent of the total number. While this amount is probably greater than the average, it shows that the larvae are very destructive in their early stages. On the average it is probable that not over 40 to 50 per cent of all the brood of the mountain pine beetle is destroyed, though no figures are available for this supposition.

In spite of the great destruction of the brood, it is doubtful if *Medetera* is as valuable a factor in controlling the brood of the beetle as is the braconid, *Coeloides dendroctoni* Cush., whose average parasitism is but about 16 per cent. Most of the larvae that *Medetera* destroys are in their early stages, and it is probable that many would have died from other causes, such as extreme temperature, overcrowding, or from other predators or parasites. Most of the larvae parasitized by *Coeloides dendroctoni* Cush. are full-grown and nearly ready to pupate, and have survived many of the hazards apt to cause their death; thus their chances of reaching maturity are considerably greater than larvae ready to hatch, or recently hatched from the eggs. A detailed study is necessary to establish these values.

RECOMMENDATIONS FOR PRESERVATION

Artificial control of the brood of the mountain pine beetle is usually accomplished by one of two methods. One consists of felling the infested trees and peeling off the bark to expose the larvae or pupae to the elements, and to ants, shrews, voles, chipmunks, etc.* The other consists of decking up the infested logs and burning them. The control work is carried on either in the spring or fall, but principally in the spring between April and the latter part of June. In a study of *Coeloides dendroctoni* Cush., which is the most important parasite of this beetle, it was found that spring control in the lodgepole pine stands destroys practically all of the brood of the parasite, and that fall control destroys only a small percentage of them. Fall control work was therefore suggested as a means whereby the braconid could be fostered. However, as the

* Rust, H. J. Progress report on the effectiveness of the peeling method of control relative to the destruction of *Dendroctonus* broods in white pine. MS. Forest Insect Field Station, Coeur d'Alene, Idaho, 1930.

females of *Medetera aldrichii* begin to oviposit immediately after the trees of either species have been attacked by the mountain pine beetle, and continue to oviposit to some extent until cold weather sets in, all of the brood of this fly in the treated trees would be destroyed by the fall control work. But spring control operations, as they are begun before the brood of the fly emerges, destroy an equal number of larvae of the fly. Because of this, it seems that early fall control work is still to be preferred, at least in the lodgepole pine stands, in spite of the destruction to the brood of *Medetera aldrichii*.

This position is also taken as neither *Medetera aldrichii* nor *Coeloides dendroctoni* Cush., the two most valuable insects in the destruction of the brood of the *Dendroctonus monticolae*, have been able to prevent outbreaks of this beetle. Though artificial control is always necessary, if the outbreak is to be controlled before too much timber is destroyed, a method of artificial control which at the same time will not injure one or both of these beneficial insects is to be desired. According to the studies of Volterra (1928) it would seem that when control work is conducted with no attempt made to protect the beneficial insects considerable harm may result in the long run. For where one animal lives at the expense of another the destruction of the host and predator in proportional numbers will cause the average number of the host to increase and the average number of the predator to decrease. If such is true, much more careful and extensive investigations should be made to determine just how control operations can be conducted so that not only will the normal average not be upset but also that the average number of preying insects may be increased above that of the barkbeetle, by a reduction in the beetle population without a reduction in the parasitoid and predator population.

SUMMARY AND CONCLUSIONS

1. *Medetera aldrichii* Wh. is the most important predator of the mountain pine beetle (*Dendroctonus monticolae* Hopk.) infesting lodgepole and western white pine. It probably destroys 40 to 50 per cent of the brood of this beetle.

2. The life cycle varied from about two to twelve months; the incubation period ranged from 10 to 14 days; the larval period ranged from one to about eleven months; and the pupil period ranged from 14 to 17 days.

3. The fly oviposits chiefly in trees recently attacked by the mountain pine beetle.

4. Spring or fall control of the brood of the mountain pine beetle by either the burning or peeling method destroys practically all of the brood of *Medetera aldrichii* Wh. Fall control, however, is probably better in the lodgepole pine stands as it destroys fewer of the brood of the most beneficial parasite, the braconid, *Coeloides dendroctoni* Cush.

5. The work of Volterra is brought in to show the danger of doing control work when no care is taken to protect the beneficial insects.

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EXPLANATION OF SYMBOLS USED IN THE ILLUSTRATIONS

- a, mandible.
 a₁, sensilla of the circular type.
 ac, anterior dorsal commissure.
 advo, anterior dorsoventral oblique muscle.
 an, anus.
 ana, antenna and parts.
 ap, anal pad.
 au₁₋₄, ventral abdominal tracheae extending to cephalized ganglia.
 b, accessory sclerite of mandible.
 bc, brain trachea.
 br, brain.
 c, central sclerite.
 c₁, sensilla of the papillary type.
 ce, sclerotized process of cuticula.
 cf, " " " "
 eg, " " " "
 ch, " " " "
 ci, " " " "
 ep, " " " "
 eu, cuticula.
 d, dorsal papilla on median piece.
 d₁, Keilin's organ.
 dc₁₋₈, dorsal commissures.
 ddvo, dorsal dorsoventral oblique muscle.
 dpvdo, dorsal posterior ventrodorsal oblique muscle.
 dvdo, dorsal segmental ventrodorsal oblique muscle.
 dvdo₁, dorsal intersegmental ventrodorsal oblique muscle.
 e, knob on median piece.
 eh, intersegmental muscle.
 f, sensilla on median piece.
 g, anterior point of median piece.
 h, lateral process of median piece.
 hd, head.
 he, horizontal exterior segmental muscle.
 hi, horizontal interior intersegmental muscle.
 i, lateral arms of median piece.
 l, intercalated sclerite.
 lt, longitudinal trunk.
 m, metacephalic rod.
 mp, median piece.

- n, ventral buccal sclerite.
 nr, nerve cord.
 p, ventral organ of maxillary palpus.
 pc, posterior commissure.
 pdvo, dorsal posterior dorsoventral oblique muscle.
 ph, pharynx.
 ph₁₋₄, tracheae supplying the buccopharyngeal muscles.
 pm₁, longitudinal pharyngeal muscles.
 pm₂, vertical pharyngeal muscles.
 ps, pseudopod.
 r, dorsal organ of maxillary palpus.
 s, salivary duct.
 s₁₋₃, sensillae of the head.
 sp, spiracle.
 t, tentorial rod.
 tr, transverse muscle.
 tgt₁₋₃, thoracic ganglionic tracheae.
 u, inner lobe of maxilla.
 v, vertical muscle.
 vdvo, ventral dorsoventral oblique muscle.
 vs, vertical segmental muscle.
 vpvdo, ventral posterior ventrodorsal oblique muscle.
 vt, visceral trachea.
 vtc₁₋₃, ventral tracheal commissures.
 vv, ventral vertical muscle.
 vvdv, interior ventral ventrodorsal oblique muscle.
 vvdv₁, exterior ventral ventrodorsal oblique muscle.
 x, pigmented area of cuticula.
 y, " " " " "

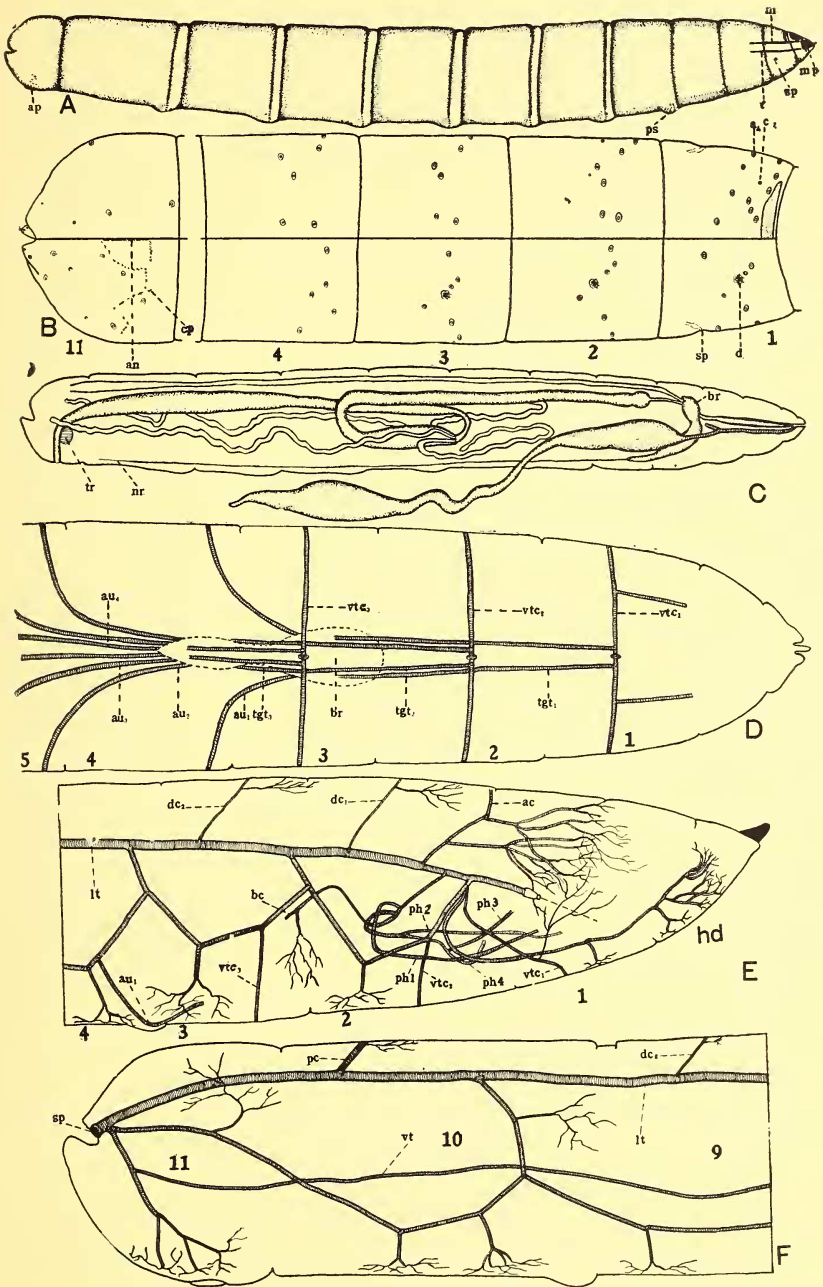
PLATE 4

Medetera aldrichii Wh.

Final Instar Larva

- A. Lateral view.
 B. The sensillae of segments 1, 2, 3, 4, and 11. Upper half, dorsal; lower half, ventral.
 C. Lateral view of internal organs, showing brain and centralized ganglia, digestive tract, Malpighian tubes, salivary glands, and heart.
 D. Ventral view of head and segments 1 to 5 inclusive, showing principal tracheae.
 E. Lateral view of head and segments 1 to 4 inclusive, showing principal tracheae.
 F. Lateral view of segments 9 to 11 inclusive, showing principal tracheae.

De Leon



MEDETERA ALDRICHI DL.

PLATE 5

Medetera aldrichii Wh.

Final Instar Larva

- A. Anterior extremity of maxillary palpus.
- B. Various types of sclerotized processes of pseudopodia.
- C. Lateral and caudal view of median piece.
- D. Posterior spiracle.
- E. Mandible and accessory sclerites; compressed laterad.
- F. Ventral view of median piece, pharynx, salivary duct, and tentorial rods.
- G. Transverse section of prothorax, slightly anterior to prothoracic spiracles.
- H. Left metacephalic rod, viewed dorsad.
- I. View of head and its parts; left, dorsal; right, ventral view.

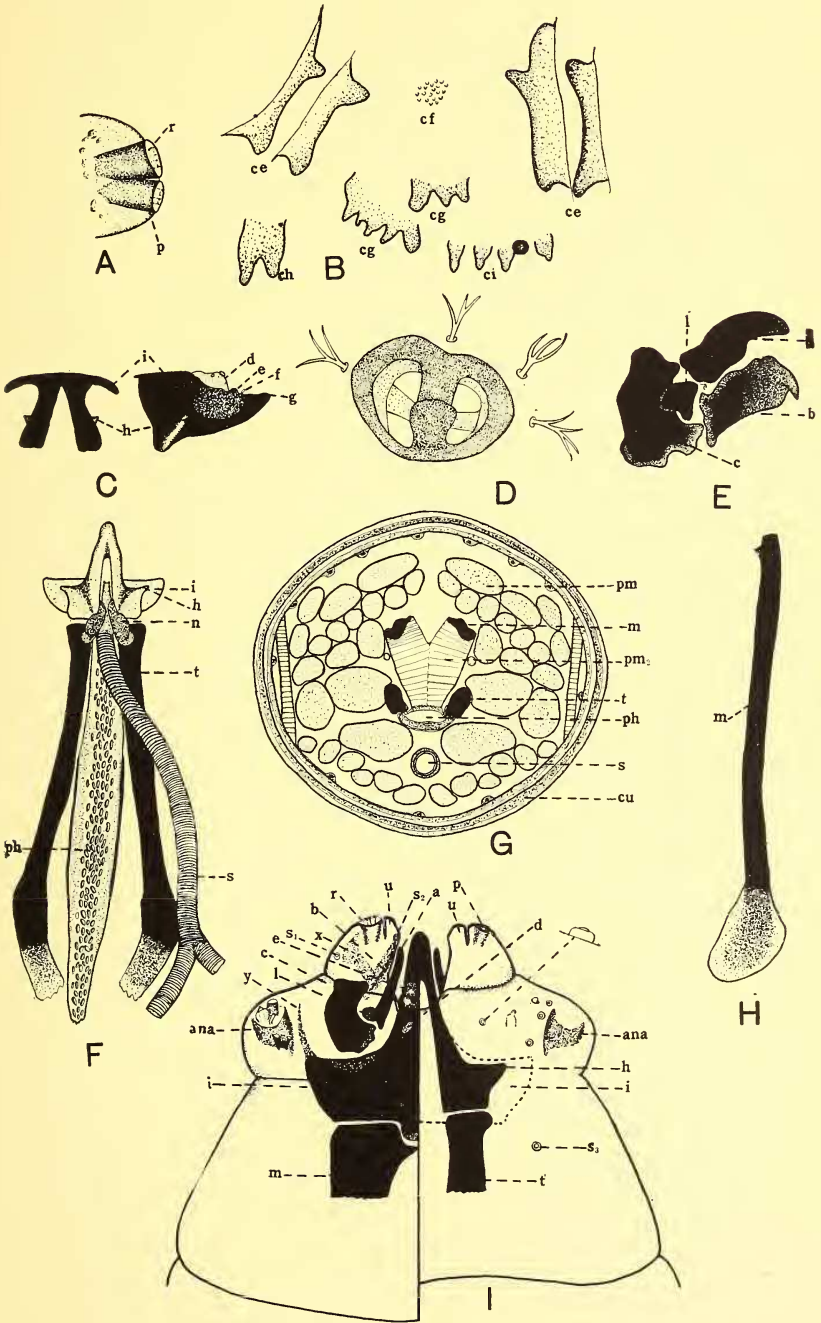
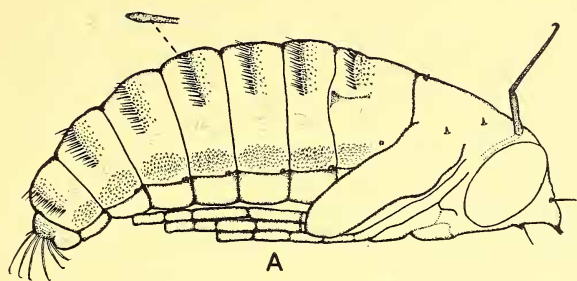


PLATE 6

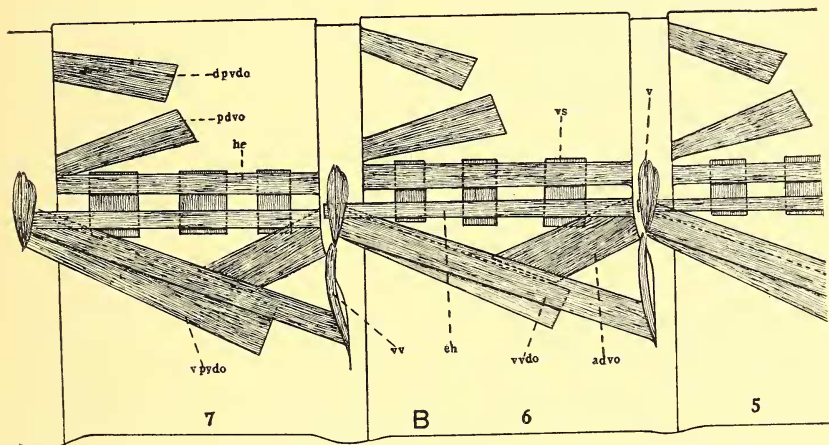
Medetera aldrichii Wh.

Final Instar Larva and Pupa

- A. Pupa.
- B. Lateral view of body segments 6 and 7, showing outermost sets of muscles.
- C. Lateral view of body segments 6 and 7, showing innermost sets of muscles.



A

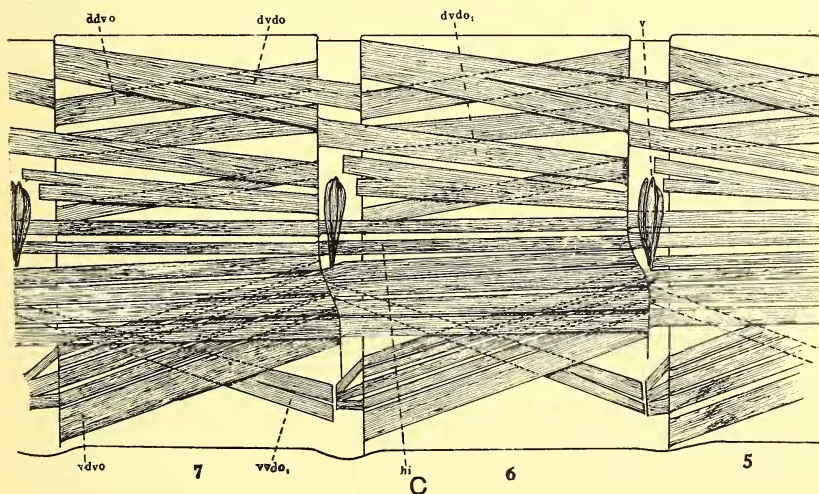


7

B

6

5



vdvo

7

vdvo₁

hi

C

6

5

PLATE 7

Medetera aldrichii Wh.

Male upper, female lower figure. The eyes in living specimens are convex, not concave as shown here.